

HARVARD BOTANI

At a meeting of the Botanical Department held Oct. 20, 1903, the following vote was passed:

"Under the head of Harvard Botanical Memoirs it is proposed to include all quarto publications issuing from the Gray Herbarium, the Cryptogamic Herbarium, and the Botanical Laboratories of Harvard University, including theses presented for the degrees of Ph.D. and S.D. in Botany. Inasmuch as some of the future publications are likely to be continuations of subjects treated in quarto papers already published, it seemed desirable to begin the numbering of the Memoirs with the year 1880, the date of the first quarto publication of any member of the botanical staff at present connected with Harvard University."

At a meeting on Nov. 25, 1916, it was voted to discontinue the series of *Botanical Memoirs*. In all, nine numbers have been issued, the titles of which are given below.

- 7. I. The Gymnosporangia or Cedar-Apples of the United States. By W. G. Farlow. Anniversary Memoirs, Boston Soc. Nat. Hist. 1880. Pp. 38. Pls. 1 and 2.
- II. The Entomopthoreae of the United States. By Roland Thaxter. Mem. Boston Soc. Nat. Hist., IV, No. 6. Pp. 133-201. Pls. 14-21. April, 1888.
- III. The Flora of the Kurile Islands. By K. Miyabe. Mem. Boston Soc. Nat. Hist., IV, No. 7. Pp. 203–275. Pl. 22. Feb. 1890.
- IV. A North American Anthurus: its Structure and Development. By Edward A. Burt. Mem. Boston Soc. Nat. Hist., III, No. 14. Pp. 487-505. Pls. 49 and 50. Oct. 1894.
- V. Contribution towards a Monograph of the Laboulbeniaceae.
 By Roland Thaxter. Mem. American Acad. of Arts and Sci. Boston. XII, No. 3. Pp. 189-429. Pls. 1-26.
 Presented May 8, 1895. Issued Oct. 14, 1896.
- VI. The Development, Structure, and Affinities of the Genus Equisetum. By Edward C. Jeffrey. *Mem. Boston Soc. Nat. Hist.*, V, No. 5. Pp. 155-190. Pls. 26-30. April,
- VII. Comparative Anatomy and Phyllogeny of the Coniferales, Part I. The Genus Sequoia. By Edward C. Jeffrey. Mem. Boston Soc. Nat. Hist., V, No. 10. Pp. 441–459. Pls. 68–71. Nov. 1903.
- VIII. The Comparative Anatomy and Phyllogeny of the Coniferales, Part II. The Abietineae. By Edward C. Jeffrey. Mem. Boston Soc. Nat. Hist., VI, No. 1. Pp. 1-37. Pls. 1-7. Jan. 1905.
 - IX. Contributions towards a Monograph of the Laboulbeniaceae, Part II. By Roland Thaxter. Mem. American Acad. of Arts and Sci., XIII, No. 6. Pp. 219-469. Pls. 28-71. June. 1908.

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A NORTH AMERICAN ANTHURUS—ITS STRUCTURE AND DEVELOPMENT.

WITH PLATES XLIX-L.

By EDWARD A. BURT.

INDEX AND TITLE PAGE OF VOL. III.

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XVIII. A NORTH AMERICAN ANTHURUS—ITS STRUCTURE AND DEVELOP-MENT.

BY EDWARD A. BURT.

LAST September, toward the close of a prolonged rain, the writer had the good fortune to find a member of this fine genus of the Phalloideae. The plant was growing in a sandy cornfield on a hillside near East Galway, New York. Gathering from the literature at hand that some genera of this family have not been satisfactorily investigated on account of the difficulty of obtaining sufficient material well preserved for study, a careful search was made which yielded thirteen mature individuals and several "eggs" in various stages of growth. This ample supply of material was preserved in alcohol and has remained in very favorable condition for determining the structural features and the development of the species.

GROSS STRUCTURE.

The general aspect of a rather old specimen of the fungus, which will be referred to throughout this article under the name of Anthurus borealis, sp. nov. (see diagnosis at the close), is shown natural size in Fig. 1. A slender clavate stipe issues from a volva, the torn apex of which is just at the surface of the ground. Both volva and stipe are white, and the latter has a pitted surface. The stipe is somewhat contracted above and then divides into six erect and narrowly lanceolate arms which bend in together at their tips. Six seems to be the normal number of these arms, but in some instances the sixth is only partially developed. The full height of the plant is from 10 to 12 cm.; the length of the arms 11-2 to 2 cm.; the diameter of the stipe is about 1 cm. below and 11-2 cm. at the broadest part above.

The back of each arm is pale flesh-colored and has a small median furrow extending its entire length. Toward the upper end of the arm the furrow is broader and very shallow, lower down it becomes narrow and correspondingly deeper, and at the base of the arm it widens abruptly, becomes very shallow, and disappears on the surface of the stipe. The lateral and inner faces of the arms are covered by the brownish olive-green

gleba (Fig. 2) until the plant reaches its maturity. Then deliquescence of the gleba occurs — accompanied by a fetid odor which is, however, perceptible for a distance of only a few feet — and the arms, upon becoming bared from their covering of spores, disclose a surface marked by irregularly branching transverse wrinkles, which do not cross the backs of the arms (Fig. 1).

Upon splitting the mature fungus longitudinally, the stipe is found to be thick-walled and with a large central cavity. The surface of this cavity is cross wrinkled (Fig. 4). A longitudinal radial section of the wall (Fig. 4) shows a cavernous structure of about three series of cavities running longitudinally and almost separated from each other, and cut up by plates and folds of the pseudoparenchymatous tissue of the wall.

Near the plane of union of the stipe with the arms a thin diaphragm, having an aperture of variable size and position, but often central, separates the main central cavity of the stipe from a dome-shaped cavity above (Fig. 4). The dome-shaped cavity is closed above, and differs from the central cavity of the stipe in having a wall with an even inner surface. Thin sheets of white tissue pass out laterally from the wall of the dome into the spaces between neighboring arms and extend vertically upward through the gleba. The plane of section for Fig. 4 is a nearly median one between neighboring arms, and cuts these sheets longitudinally in areas marked T, Fig. 4. The gleba is here marked g. The hymenial surface is borne upon a very complicated system of folds and pockets, or closed chambers, of this tissue (h, Fig. 20), as will be described further on.

The spores (Fig. 12) are apparently olive-green, simple, ellipsoidal, $3.4 \mu \times 11.2 \mu$. They are borne in clusters of from 5 to 8 at the ends of slender basidia which are divided into 4 or 5 short cells and are constricted at the septa (Fig. 11). But this is also considered again further on.

A median longitudinal section through the arm and the dome (Fig. 5) shows that the inner face of the arm is adnate to the dome for about one sixth of the length of the arm. This results in confining the gleba in this lower portion of the arm to the spaces between the lateral faces of the arms (Fig. 8). There exists here in the lower portion of each arm the condition which Patouillard has shown to exist in *Lysurus mokusin* (Cibot) Fr. throughout the entire length of the arm.

Each arm is hollow (Fig. 5). Its outer and inner surfaces are approximately parallel, the wall being really thrown into transverse folds rather than merely wrinkled in its outer surface as seems to be the case when viewed externally after the deliquescence of the gleba.

¹ Patouillard: Fragments mycologiques; X. Organisation du *Lysurus mokusin* Fr., p. 65-70. And also Journal de botanique, 16 Juillet, 1890, p. 252.

At the sides of the dome and near the diaphragm, two smaller cavities may be seen (Fig. 4). Passages are shown leading out from each of these. The passage k near the diaphragm leads into a similar small cavity in the next space between two arms. By a series of six such small cavities and connecting passages a complete circuit is made through the wall of the stipe at its upper end. Each of the small cavities is in communication with the large cavity of each of the two adjacent arms above by passages marked l. Irregularly shaped small cavities extend from the ring-like system just described down into the wall of the stipe. This system of cavities does not show in this region any direct connection with the cavity of the dome or with the main central cavity of the stipe.

The course of these cavities from the chambers in the wall of the stipe up into the arms is of special interest as showing the arrangement and distribution in early stages of the bundles of hyphae which then filled these cavities. But this subject will come up again in tracing the development of the plant.

The so-called "eggs" are found underground either singly or in clusters of from two to four upon branching mycelial strands (Fig. 3). In the fresh condition they vary in form from nearly spherical to oval, but upon lying in alcohol they contract more in transverse than in longitudinal diameter. An "egg" just beginning to rupture at the apex had a diameter of 2 cm. The wall of the peridium has the usual structure of three layers, of which the outer and the inner are thin white membranes, but composed of very different hyphae however. These layers are separated by a broad layer of gelatinous tissue (M', Figs. 7-9).

HISTOLOGY AND DEVELOPMENT.

The Mycelial Strand.

Full-grown mycelial strands upon which the "eggs" are borne may have a diameter of 2 mm. These strands show a broad medullary layer of fine hyphae running longitudinally and a narrow cortical layer consisting of hyphae more irregular in their form and course, more interwoven, and with occasional short lateral branches extending outward to the surface of the strand. There is no sharp separation of these layers—the medullary layer passes gradually into the cortical.

Crystals of calcium oxalate have been found in the cortical portions of some members of the Phalloideae, as by De Bary¹ in *Phallus caninus* and by Fischer² in *Clathrus can*-

¹ De Bary: Beitr. z. morph. u. physiol. der pilze. Zur morph. der phalloideen, p. 59.

 $^{^{2}}$ Ed. Fischer: Untersuch. z. entwick. der phalloideen, p. 3.

cellatus. Such crystals occur in the cortical portions of Clathrus columnatus Bosc., specimens of which, collected in Florida, I have been enabled to examine through the kindness of Professor Farlow. The Anthurus shows no crystals.

The Youngest Egg Found.

The youngest egg of the Anthurus material, after lying in alcohol, was elliptical in median longitudinal section, being about 6 mm. long by 3 mm. wide. After staining with carmine and imbedding in paraffin, one half was cut into longitudinal sections and the other into transverse sections.

In this stage of the egg the two tissues of the mycelial strand can still be made out, but they are undergoing such differentiations as already to show recognizable early conditions of most parts of the mature plant. The stipe is here a slender body extending from the mycelial strand to the central part of the egg (Fig. 14). This central portion consists of the gleba g and fundament of the arms a'. Surrounding these structures is a broad layer M' somewhat horseshoe-shaped in the section and constituting the principal mass of the egg. This becomes the gelatinous layer of the peridium.

The structure of this egg in detail is as follows:—

The medullary tissue of the mycelial strand is prolonged up through the stipe in a bundle of slender longitudinally running hyphae, marked M. This bundle is, for the most part, separated from the fundament of the wall a by a slight space, but at some points single hyphae and small bundles run obliquely upward across the space and up along the wall (Fig. 15). Near the lower end of the stipe medullary hyphae pass into the wall.

Toward the central part of the egg the hyphae of the bundle M spread out in a sheaf-like manner and form an early stage of the gleba and its supporting structure. At n, Figs. 14 and 16, the medullary hyphae from the gleba may be seen running out directly into the broad layer M', which has been mentioned as becoming the gelatinous layer of the peridium.

The layer M' is already somewhat set off from the tissue of the gleba by very fine hyphae which stain more deeply with the carmine than does the surrounding tissue, and which lie in a very thin and open layer covering the future gleba and arms, and pass perpendicularly through the masses of hyphae n connecting the gelatinous layer M' with the gleba tissue. This thin layer of rather scattered hyphae is the beginning of the inner wall of the peridium (i, Figs. 15–16). Under higher magnification (Fig. 17), this layer may be seen to receive some of its hyphae from the gleba tissue, where they seem to have a subhymenial position.

Of the tissues already considered, the bundle forming the axis of the stipe, the

gleba, and the gelatinous layer of the peridium, are direct continuations of the medullary tissue of the mycelial strand and must be regarded as of medullary origin. The inner wall of the peridium has the same origin probably on account of its subhymenial connections.

The cortical tissue of the mycelial strand is continued in the thin outer layer of the egg (C, Figs. 14 and 16). The hyphae of this layer have become more irregular in form, and branch and change their course so as to become extremely interwoven. The tissue remains loose, and must allow circulation of air throughout its whole extent. By referring to the cross section (Fig. 16), portions C' of the cortical tissue may be seen extending inward from the main peripheral mass of this tissue to the gleba. There are six of these portions placed at about equal distances apart in the cross section. They have the position of walls or plates extending from the base of the egg longitudinally upward to a short distance above the gleba mass, and extending inward from the peripheral layer to the fundament of the stipe and arms. In all of the lower and middle portions of the egg, these plates of cortical tissue divide the gelatinous layer M' into six parts, the hyphae of which do not cross through the partition from any part into the adjacent one. The partitions do not extend to the apex of the egg — at least not in this nor in the more advanced stages which I have examined. Above the level of the upper ends of the arms, the portions extend inward from the cortex only a part of the distance to the axis, and the amount of this inward extent diminishes rapidly higher up, so that near the apex of the egg the partitions become so shallow as to be hardly more than traces along the inner face of the cortical layer. It follows from this that in the upper part of the egg, there is but a single mass of the gelatinous layer M' and that this is divided below by the cortical partitions into the six masses already mentioned.

In the lower third of the egg, there is a cylindrical layer of tissue (C", Figs. 14 and 15) similar to that of the partitions and into which they pass. This layer completely surrounds the fundament of the stipe and wholly separates it from the gelatinous layer of the peridium. Toward the inner face of the layer C", its hyphae anastomose less frequently and are less branched, but become closely and irregularly laterally inflated. In preparations stained with paracarmine alone, the walls of these hyphae were but slightly stained as compared with their protoplasmic contents. In such preparations the greater masses of protoplasm at the inflated portions gave to the hyphae a dotted look under low and medium magnification (p, Figs. 14 and 15). In the double-stained preparations with the cell-walls well brought out, these hyphae appeared under high magnification as shown in x and x', Fig. 18.

The inflated hyphae do not wholly compose the fundament of the wall of the stipe; small bundles of fine hyphae b are also present but cannot be traced long distances. These uninflated hyphae are undoubtedly of medullary origin, as they closely resemble the medullary hyphae of the main cavity of the stipe, and, as stated in a former place, similar bundles of hyphae pass from the medullary portion into the wall of the stipe near its base. The inflated hyphae seem to occupy the spaces between the bundles of uninflated medullary hyphae in the fundament of the stipe.

The stipe seems to be composed in part of tissue of medullary origin, and in part of tissue of cortical origin. Later stages of the egg show that the medullary tissue of the wall becomes the gelatinous tissue of the chambers and finally disappears, while the inflated hyphae of cortical origin differentiate further into pseudoparenchyma.

The arms of the receptaculum are borne upon the upper end of the wall of the stipe. In this stage of their development, they consist of six large masses of longitudinally running hyphae (a', Figs. 14-17) passing upward from the fundament of the wall. In the lower part of each mass, the tissue is very dense and seems to consist of both the medullary and cortical tissues of the stipe wall but with the medullary hyphae collecting into the centre of the mass. Further up the hyphae of the mass seem to be wholly of medullary nature. Each of these masses is the fundament of an arm and lies in a V-shaped cavity extending upward along the surface of the gleba (Figs. 14-17). The arm is in contact with the supporting tissue of the gleba near the lower end—at about the region of the future dome; but I cannot detect any hyphae passing from the one structure into the other here.

The arms arise at the inner edges of the cortical plates (Figs. 16-17). Hyphae from these plates cross the narrow separating space and come into contact with the fundament of arms. I am inclined to think that these hyphae merely reach the fundament and do not enter it, and that we have here; for this part of the arm, the first penetration of the cortical tissue into and across the narrow surrounding space which this tissue takes full possession of later on and in which it builds up the wall of the arm.

The surface of the cavities in which the arms lie is lined by a palisade-like layer of cells closely packed together, which stain deeply with the carmine. They are the swollen ends of branches given off by the spreading hyphae of the medullary system. This layer of cells is the young hymenium (h, Figs. 14-17), and the swollen cells are the young basidia. This hymenial layer is thrown into a series of folds which, judging from serial cross sections, extend principally in a longitudinal direction and have their hollows directed somewhat centripetally in between the radiately spreading hyphae of the gleba

(Figs. 16 and 17). In some places these folds have their surface thrown into a secondary series. Here the small depressions of these folds extend into the primary fold in the direction that the hyphal branches must have originally taken in passing toward the surface of the cavity from the deeper tramal tissue of that primary fold. The impression gained from the branched structure of the chambers is that originally simple chambers have had branches form in the tissue of the gleba through the gradual spreading apart of the masses of hyphae which reached to the surface of the first chambers, and that this spreading apart followed from the need of a greater surface consequent upon the abundant production of basidia in the region of the existing chambers. That the formation of the basidia causes the formation of branches of the chambers, seems to be shown by the fact that the most remote portions of the branchchambers are constantly lined with the basidia. That the basidia form only in the region of already existing chambers seems to be shown by the fact, that upon running through the series of cross sections, small chambers are not found absolutely isolated from the large chambers. They may seem so isolated in some sections, but others show the connection.

How has there arisen from the simple conditions of the cortical and medullary tissues in the mycelial strand the more complicated and yet symmetrical disposition of these tissues in the egg just described? How have the six masses of the gelatinous layer of the peridium come to be separated from each other by plates of cortical tissue? How happens it that these masses of gelatinous tissue are connected with the medullary tissue from which they originate, only in the upper part of the egg? Was there a connection down to the base in a younger stage?

Determination of Earlier Development by Reference to Clathrus.

No younger egg of Anthurus is available for a direct answer to these questions, yet the stage of development just described bears in certain features so much in common with the better known genus Clathrus that approximately correct answers may nevertheless be had.

The earlier conditions of Clathrus cancellatus have been examined and illustrated by Fischer. His earliest stage (Taf. 1, fig. 1) shows the medullary tissue of the mycelial strand spreading out in the pyriform egg and sending several radiating branch-like masses into the cortical region. Broad masses of cortical tissue occupy the spaces between these branches. In a slightly older stage the medullary branches have by growth become much broader in their peripheral portion and have crowded the separating

¹ Ed. Fischer: Untersuch. z. entwick. der phalloideen, p. 3, taf. 1 und 2, fig. 1-7.

cortical portions into narrow plates. These stages bring the development up to the conditions shown in Fischer's Figs. 3 and 4, which are quite similar to my Fig. 16 except perhaps in the case of the fundament of the arm.

These early stages of *C. cancellatus* rather indicate that the arrangement in the peridium of masses of gelatinous tissue separated from each other by plates of cortical tissue has resulted from the extrusion into the early cortical layer of masses of more vigorously growing medullary tissue; still such stages do not forbid the interpretation that the cortical tissue has taken the initiative and has intruded into the medullary region forming the plates.

The supply of Clathrus columnatus Bosc., to which reference has been made on a preceding page, contained one egg in an earlier stage than those of C. cancellatus described by Fischer. Clathrus columnatus in its mature form is characterized by a receptaculum having usually four meridionally ascending arms which are joined together into two opposite pairs above, and then these pairs are joined together by a single connecting portion. The youngest egg of this species, as taken from the alcohol, was pyriform in general form (Fig. 19) and somewhat tlattened on two opposite sides, so that a cross section would be elliptical rather than circular. Four well-marked ridges run meridionally and are separated from each other by furrows. Upon sectioning this egg it was found that these ridges are wings of the medullary tissue. The cortical tissue of the furrows is especially loose, and hyphae from two opposite sides seem to be bridging and filling in the furrows. But the important feature is, that the outer surface of the cortical layer conforms to the ridged medullary surface to a much greater degree than in later stages, thus indicating that the medullary layer has taken the initiative in the disposition of the tissues of the egg.

The question in regard to the arrangement in *C. columnatus* of the gelatinous layer of the peridium in four masses—as in most cases—separated from each other throughout by four plates of cortical tissue, may be answered by stating that it has resulted from the extrusion of the medullary tissue along four longitudinal lines out into the cortical region. Here the entering masses have broadened out in their peripheral portions so as to crowd the cortical portions between the masses into narrow plates. The answer to this question for *Anthurus borealis* is somewhat the same, but is complicated by the generic differences between Clathrus and Anthurus. In *C. columnatus* the cortical plates extend from the base to the apex of the sporophore, cutting off all direct connection of one gelatinous mass with its neighbors. This indicates that the medullary extrusions were strictly lateral. In *A. borealis*, it has been pointed out that the six cortical plates do not extend to the apex of the sporophore, and that the six gelatinous masses are in direct connection with each other above and also have radial connection with the medullary tissue of the gleba along six lines (n, Fig. 16). Such connections indicate

not only that in this species medullary extrusions have occurred laterally along six longitudinal lines in the region of the arms, as in the Clathrus, but that such extrusion upward and outward has also occurred from the upper end of the medullary column.

With regard to the last question, as to whether in an earlier stage the gelatinous masses of the peridium were connected down to the base with the column of medullary tissue in the main central cavity of the stipe, I think that an answer in the negative may be safely ventured. C. columnatus has such connections, and they determine the mature form of the fungus. Were such connections originally present in A. borealis, some slight indications of the fact, as by the directions of the hyphae, or by some slight persisting connection, as by breaks in the uniformity of structure of the fundament of the wall of the stipe, would have been found in some of the sections. After passing into the cortical region, the medullary masses must have crowded their way downward into the cortical tissue by the means that in C. cancellatus has compressed the broad masses of cortical tissue shown in Fischer's Fig. 1, of his work already referred to, into the compact plates of his Fig. 2. That the medullary tissue which becomes the gelatinous layer of the volva may crowd its way down into a loose pre-existing tissue was shown by De Bary in his careful observations upon the egg of Phallus caninus. But it is quite probable that the greater portion of the length of the gelatinous masses below the level of the arm is to be accounted for by the fact that the arms were at a much lower level when extrusion of the masses occurred, and that while they have retained their connection with the gleba, they have also grown and lengthened with the growth of the stipe and the egg in general.

Development of Anthurus in Next Older Egg.

Let us now pass to the later development of Anthurus. A more advanced stage than that already considered is shown in Fig. 20. This represents in cross section one of the arms, the surrounding gleba, and the cortical plate passing from the arm through the gelatinous layer of the volva to the cortex. The location of the figured portion in the entire cross section may be seen by reference to Fig. 7, although this latter is from a still more advanced stage of the egg.

In Fig. 20, one is struck by the great development of the gleba, as compared with that in Fig. 17. Still the repeated formation of new series of folds upon the surface of those already existing would ultimately give a very intricate structure. Indications of such a method of folding were afforded by the younger stage. The great number of small closed chambers shown in this section and in those of later stages seems to show that

De Bary: Beitr. z. morph. u. physiol. der pilze, 1. Reihe, p. 194, taf. 29, fig. 3 und 4.

some other factor than repeated folding has aided in their formation. The cavities between the primary and secondary folds of Fig. 17 can now be followed only with great difficulty, and in these cases they seem to be rows of small closed chambers with occasional connecting passages. These systems of cavities are also frequently cut off from reaching quite up to the wall of the arm, which is now developing in the narrow space about the fundament of the arm of the younger stage. All of the chambers in that stage opened into this space.

The breaking up of the earlier communicating chambers into the many small chambers of this section, seems to indicate that at those places in which changes occurring in the gleba have caused folds to be crowded into close contact, hyphae from the tramal tissue of the one fold, or of each fold, pass into the other and bring about an anastomosis of the folds. Indications of such anastomoses in formation are not infrequent. In his study of *Ithyphallus tenuis* Fischer¹ pointed out that it may be that anastomosis of neighboring folds is a factor in the formation of the closed chambers of the gleba.

The deeply staining cells of the hymenial layer are now more elongated and are basidia, bearing a cluster of spores at their outer ends. These basidia already show the series of constrictions which become so singular a feature in later stages.

Great development of the arm has been taking place. It now fills the whole of the cavity which in Fig. 17 was only partially occupied by its fundament, and is in close contact with the folds of the gleba. Two quite distinct tissues now compose the arm. There is a central mass of fine hyphae running mostly in a longitudinal direction. This tissue is highly gelatinous and, in the double-stained preparations, takes the same orange color that is taken by the gelatinous layer of the peridium, by the tramal tissue, and by the central tissue of the stipe,—all of which are of medullary origin.

The second tissue of the arm surrounds the gelatinous constituent. It consists of a narrow layer of hyphae connected with the tissue of the cortical plate. These hyphae are branched and irregularly inflated, and are developing into the pseudoparenchyma. This tissue retains in the double-stained preparations the purplish red color given by the carmine, and is sharply distinct from the gelatinous tissue of the arm on the one side and from the gleba on the other. It seems to find conditions for its development most favorable along the surfaces of contact with the gelatinous tissue of the arm and with the gleba rather than midway between these two surfaces. This causes a rather more compact arrangement of this tissue next to these surfaces than in the middle of the space between them. This appearance has been referred to repeatedly by Fischer, and it is probably this which gave him

¹ Fischer: Entwick. der fruchtkörper einiger phalloideen, p. 12, taf. 2, fig. 12. In Annales jardin botanique Buitenzorg, vol. 6.

the idea that the pseudoparenchyma develops from the hyphae both of the gleba and of the gelatinous mass of the arm. The hyphae of this narrow layer are, however, in direct connection with the hyphae of the cortical plate and through that with the cortical layer, and stain the same.

In Fig. 21, the small portion y of Fig. 20 is shown more highly magnified. On the one side may be seen the gelatinous tissue of the arm, on the other there are the tramal tissue and the hymenial surface with its constricted basidia here without spores. In the space between may be seen the coarser and more irregularly shaped hyphae of cortical nature, marked with irregular lateral inflations and taking on the form of intermediate conditions of pseudoparenchyma. I am unable to find, in any of the many sections examined, hyphae passing from the gelatinous tissue of the arm on the one side or from the gleba on the other into the space between, and there forming pseudoparenchyma by abjointing or constriction of their swollen tips.

The wall of the stipe is now in an instructive stage of development. Serial radial longitudinal sections are shown in Figs. 22 and 23. Two quite distinct tissues are present, as was pointed out in the younger stage. One of these consists of hyphae running in general in a longitudinal direction. These resemble the hyphae of the main cavity of the stipe and those of the gelatinous tissue of the arms. At most places in the section, of which only a small portion has been drawn, these hyphae are in small oblong or linear masses separated from each other by a more deeply stained tissue. The oblong masses lie in chambers which become empty at the time of elongation of the stipe. The deeply stained walls of the chambers are not yet folded; they consist of an early stage of pseudoparenchyma.

Although at some places in these sections and often in whole sections (Fig. 23), the oblong masses of hyphae in the chambers seem to be completely cut off from other masses of similar nature by the chamber walls, yet the examination of the preceding or following sections in the series will show small openings in the walls through which hyphae pass from chamber to chamber. Such an opening is shown at z, Fig. 22. This section was next in the series to that represented by Fig. 23.

Sections of the middle and upper portions of the stipe do not show bundles of hyphae passing from the medullary tissue of the main central cavity outward into the chambers of the wall. But near the base fewer layers of chambers occur in the wall, and bundles of hyphae do pass from the medullary tissue of the axis into the chambers through small openings in their walls. Such entrance of the medullary tissue into the chambers may be seen at the points b'', Fig. 10, which represents a median longitudinal section through the base of an egg in a still older stage of development.

From the above observations it may be concluded that near the base of the egg, bundles of medullary hyphae pass into the fundament of the stipe, branch there perhaps, and become loosely interwoven; at the place of origin of the arms, these bundles are crowded together more compactly — probably by the extrusions of medullary tissue in forming the gelatinous layers of the peridium — and ascend in six masses, each of which is the fundament of an arm. All of these bundles of hyphae gelatinize and disappear ultimately, and leave empty chambers: hence the course of this tissue from the chambers of the stipe-wall up into the arm is shown by the connection of the cavity of the arm with the cavernous structure of the chambers of the wall of the stipe, reference to which was made in describing the structure of the mature plant.

The second constituent of the wall of the stipe is, in the stage represented by Figs. 22 and 23, more distinctly seen to be in connection with the surrounding sheath of cortical nature than in the younger stage of Figs. 14-17. Its hyphae are differentiating into pseudoparenchyma by the formation of irregular lateral inflations, as described in the case of the wall of the arm.

Fischer has stated for Clathrus cancellatus and several Phalleae that the hyphae of the chambers radiate outward and form their pseudoparenchyma walls from their swollen tips, contribution to these walls being also made in various Phalleae by similarly swollen tips from medullary hyphae of the main central portion of the stipe on the one side of the stipe-wall and from the primordial tissue (my cortical sheath) on the other. In thick sections there is somewhat of the appearance which he describes and figures repeatedly, but it is due to the packing together of the pseudoparenchyma next to the surface of the gelatinous tissues - to which reference was made in the case of the arm — and to the impossibility of determining with certainty in such sections the real connection between the cell-like pseudoparenchymatous bodies. But even here I can in no case find a hypha from the medullary tissue of the main central cavity of the stipe or from the chambers of its walls making a distinct connection with the pseudoparenchyma - such a connection as is easily seen between the tramal tissue and the basidia. In sections cut 6 2-3 μ thick, it may be seen that the pseudoparenchymatous hyphae run in the plane of the wall and not perpendicularly into it, as would be the case provided they had the origin which Fischer has stated.

The conditions which I have described stand out still more distinctly, when such a thin section, after removal of its paraffin and after being run down to water but not fixed to the slide, is then treated with a drop of dilute potassium hydrate. The section should be carefully crushed under the cover-glass so as to spread it out somewhat and

¹ Fischer: Untersuch. phalloideen, p. 5, 6, and 36, and fig. 26, 27, and 32; and Zur entwicklungsgesch. der fruchtkörper einiger phalloideen, p. 17, and fig. 18.

separate its hyphae to a slightly greater extent, and finally stained with aqueous solution of safranin. The hyphae of the chambers will be found quite free from the strands of pseudoparenchyma, while the hyphae of the latter will now be separated sufficiently to show with greater distinctness such conditions of development as have been drawn at x'', Fig. 18.

Final Development.

Such an intermediate stage of the pseudoparenchyma leads up to its final condition shown in Fig. 10. The walls of the chambers are no longer straight as in Figs. 22 and 23, but are thrown into folds closely crowded together (Fig. 10, p).

The structure of the wall of the stipe affords the clue to the formation of these folds. The branched and interwoven bundles of medullary hyphae b make the elongation of the chambers dependent upon the elongation of this medullary tissue during its existence. The more rapid growth of the pseudoparenchyma in the chamber walls tends to make these walls longer than the chambers can become during the existence of their medullary contents. The excess in length of the walls is laid down in the folds.

Elongation of the Stipe.

When the gleba has attained its maturity and the stipe has completed its folded walls, a series of changes occurs in the egg provided external conditions are favorable. Through these changes the elaborately constructed receptaculum bursts from the volva, and rises aloft, conspicuously exposing its spores to the disseminating agency of insects. These changes are:—

- a. The gradual elongation of the egg from its nearly spherical form in early life. During the later stages of this elongation, the volva separates from the receptaculum by the splitting of the inner wall of the peridium (i, Fig. 9).
- b. The gelatinization and disappearance of the medullary tissue occupying the main central part of the stipe, the chambers of its walls, and the interior of the arms. (The beginning of this change is shown by the main central tissue of the stipe in Fig. 9.) This permits
 - c. The straightening out of the folds in the walls of the chambers.

As a result of these changes, the receptaculum pushes upward against the apex of the peridium, or volva, which becomes thinner there (Fig. 9) and is ruptured finally. The receptaculum then emerges. These changes occur in wet weather.

The straightening out of the folds in the chamber walls of *Phallus caninus* and of *Phallus impudicus* was stated by De Bary to be due, in his opinion, to the inflation of

the chambers by the formation of a gas within them.' This idea has found its way into the text-books.² Such an explanation of the phenomenon has been objected to, and very properly so, by Fischer in a short paper of great importance.³

In this article Fischer points out that the chambers are not surrounded by air-tight walls; that all of the chambers are open on one side in some of the forms which he has studied; and that there is no visible indication of the inflation of the chambers during their elongation. From these facts he concludes that the walls are not passive in their straightening out, as De Bary's explanation necessitated.

That they are the active agents he deduces from the forms of the cells at the ends of the folds and from their changes in form when the folds straighten out. He shows that at the inner angle of the fold the cells are wedge-shaped as if by compression, while on the periphery of the fold they are elongated and thin as though stretched out there. Upon placing such folds in certain aqueous solutions of slight density, the turgescence of the cells increases by absorption of the liquid, they become more nearly spherical, and the effect of such change of form both at the inner angle of the fold and at its periphery is to straighten out the fold.

In Anthurus borealis the cells of the folds have the forms which Fischer figures and the folds straighten as he states. As the elongation of the stipe in plants of this sort occurs only in wet weather or in damp places, it seems to me that Fischer has offered the true explanation of the rapid elongation of the stipe—so rapid as to give rise to the popular impression that such plants attain their full growth in a night.

The Hymenium.

It has been stated that the hymenial layer lines the chambers of the gleba. The hyphae of the trama give off numerous short lateral branches, the swollen ends of which form the hymenial layer (h, Figs. 17 and 20). In the youngest egg of Anthurus these swollen ends were unsegmented and did not yet bear spores, and they stained deeply with the carmine. In the later stages spores were present, and the deeply stained and swollen but nevertheless comparatively small and slender ends of the tramal branches were divided into four or five short cells and constricted at the septa (Fig. 11).

It may be urged that the end cell of this series should be regarded as the true basidium, but the preparations do not favor such a view. The figure was carefully made

¹ De Bary: Beitr. z. morph. u. physiol. der pilze, I., p. 202 and 207.

²(a) De Bary: Comp. morph. of the Fungi, etc., Eng. trans., p. 323. (b) Sachs: Text-book of botany,

Eng. trans., p. 341. (c) Goebel: Outlines of classif. and spec. morph., Eng. trans., p. 139.

³ Ed. Fischer: Bemerk. über den streckungsvorgang des phalloideen-receptaculums. Mittheilungen der naturforschenden gesellschaft in Bern, 1887, p. 142-157.

with the aid of an Abbé camera lucida, and shows accurately the differences in form between the branched tramal hypha and the constricted basidium. But there are also differences in nature between the two, which are revealed by the action of stains. The tramal hyphae and their short branches as far as the first cell of the basidia stain but very slightly with carmine or eosin, while the 4- and 5-celled basidium stains intensely with these substances and its parts all stain alike, the terminal cell not differing in nature from the three or four below.

This character of the basidia seems to be unique—at least so far as my reading and observation go. Still it may have been overlooked in other cases. It is readily demonstrated by crushing under a cover-glass sections that have been treated with potassium hydrate and then staining them with aqueous solution of eosin.

No cystidia were to be seen. In my Fig. 11, I have omitted drawing the spores on one basidium, but that was for clearness in the figure. The sterigmata are very short, and the spores are borne in a close cluster of from 5 to 8 at the obtuse end of the basidium. The spores are olive-green, simple, ellipsoidal, $3-4 \times 11-2 \mu$. Throughout the gleba they all seem to be in about the same stage of development and all ripen together probably. No attempt has been made to germinate them.

Clamp Connections.

A form of clamp connection may be seen in the earlier stages of the egg. It was observed very frequently in the medullary tissue of the axis of the plant and in the gelatinous tissue of the peridium and more rarely in the cortical layer. In the latter case hyphae having such connections showed fewer anastomoses with the other hyphae and were more regular in form than is the case usually with the cortical hyphae. In this form of clamp connection one or both of the adjacent cell ends are very considerably swollen. Fig. 13 a shows one of the cases in the cortical layer and Fig. 13 b, two in the gelatinous layer of the peridium.

Summary of Development.

- 1. All of the tissues of the egg arise from internal differentiation of the medullary and cortical tissues of the mycelial strand. In such differentiation
- (a) The medullary portion gives rise to the column of gelatinous tissue in the main cavity of the stipe, to the more persistent forms of this tissue which constitute the diaphragm and the dome, to the entire mass of the gleba, and to the gelatinous and inner layers of the peridium; while
- (b) The cortical layer gives rise to the outer wall of the peridium, to the cortical plates (or radial walls), and to the cortical sheath of loose tissue outside of the stipe.

- 2. The receptaculum is formed by the joint action of both the cortical and medullary tissues. Of these the cortical constituent develops into the pseudoparenchyma of the walls, while the enclosed medullary bundles of the chambers finally become gelatinous and disappear, their most manifest function being apparently that of preventing the elongation of the chambers until the completed formation of the folded walls of pseudoparenchyma has provided a mechanism for quickly raising the gleba aloft at maturity under suitable conditions.
- 3. The straightening out of the folds in the elongation of the stipe seems to be due to turgescence of the cells at the ends of the folds, as first shown by Fischer, and not due to inflation of the chambers by a gas.

METHODS USED.

The material was stained in bulk with Mayer's paracarmine.' This penetrated well and gave quite satisfactory results. It was necessary to use an alcoholic stain on account of the gelatinization of the medullary tissues when left in bulk in an aqueous stain for more than a few minutes. After dehydration the material was cleared in oil of cedar-wood or in chloroform and imbedded in paraffin. The sections were mounted on the slide with Mayer's albumen medium. After removal of their paraffin with xylol, they were run down through the grades of alcohol to water and then stained on the slide from 1 to 5 minutes in a dilute aqueous solution of safranin. After washing with water, the series were then mounted in a dilute glycerine consisting of two volumes of concentrated glycerine and one volume of distilled water. An excess of this mounting medium was used, and it was allowed to concentrate for several days by evaporation from under the edge of the cover-glass. Sealing such large mounts is often troublesome. After cleaning they were closed with hot glycerine jelly and then finished with Bell's cement, after the method recommended by Lee.²

The attempt was made to stain the sections on the slide when brought to the proper grade of alcohol with the mixture of alcoholic safranin and anilin water, after the formula of Zwaardemaker,³ but the differential stain obtained was not so satisfactory as with the aqueous safranin.

The use of Canada balsam, in order to save some of the labor of mounting long series in glycerine, had to be given up as the true relations to one another of hyphae lying in different planes were less satisfactorily shown in that medium than in glycerine.

¹ P. Mayer in Mitth. zool. stat. zu Neapel, X, 3, 1892, p. 491; also in Lee: Microtomist's vade-mecum, 3d ed., p. 106.

² Lee: Microtomist's vade-mecum, 3d ed., p. 252 and 254.

³ See Lee: Microtomist's vade-mecum, 3d ed., p. 65.

HISTORICAL AND SYSTEMATIC ACCOUNT.

There is but little literature upon Anthurus, and what there is has been confined almost wholly to brief systematic descriptions of the mature forms of the few species. The earliest form described was Lysurus archeri Berk., collected in J. D. Hooker's Antarctic voyage of discovery, 1839–1843. This form was afterward figured by Berkeley in Flora Tasmaniae, Vol. II., 1860, Tab. 184. From the illustration of an "egg" given there, Fischer was able to decide in 1889 that in Anthurus the arms inclose and arch over the gleba in the young stage. This seems to be all that has been heretofore directly known in regard to young stages of Anthurus.

According to the view of the genus Lysurus presented by Fischer in Saccardo's Sylloge fungorum,² A. borealis would be considered a Lysurus, for its arms bend inward—not outward.

Patouillard³ has, however, recently objected to such a view of Lysurus and shows from late studies upon a supply of *L. mokusin* collected in China by Delavay, that the marked characters of that species are the smooth inner faces of the arms and the presence of the gleba upon the outer (externe) faces of the arms. An Anthurus, he states, has its spore mass against the inner faces of the arms. This objection has caused Fischer to modify the characters of the two genera in a late addition to his monograph upon the Phalloideae,⁴ so that now he distinguishes Lysurus from Anthurus by the former having the inner faces of its arms smooth and not covered by the gleba, while they are so covered in Anthurus.

Upon such a view of the genera our North American fungus must be regarded as an Anthurus, for the greater portion of the inner face of each arm is cross wrinkled and is in contact with the gleba. It approaches Lysurus in having the lower portion of the inner face of each arm smooth and not covered by the gleba. The erect position of its arms also is like that of *L. mokusin*.

This species thus comes to have an important systematic interest from its closely connecting Lysurus with Anthurus and so with the Clathreae, where Fischer places it.

The fungus is quite distinct from all forms heretofore described and may be regarded as a new species with the following diagnosis:—

¹ Ed. Fischer: Untersuch. z. entwick. der phalloideen, p. 11.

²Saccardo: Sylloge fungorum, Vol. 7, p. 22.

³ Patouillard: Organisation du *Lysurus mokusin* Fr. Journal de botanique, 16 Juillet, 1890, p. 252.

⁴ Fischer: Neue untersuch. z. vergleich. entwicklungsgeschichte u. systematik der phalloideen, p. 6 and 27.

ANTHURUS BOREALIS, sp. nov. Plates 49 and 50.

Solitary or subcaespitose. Stipe white, clavate, divided above into 6 erect, narrowly lanceolate, hollow arms incurved above, and with pale flesh-colored backs which are traversed their entire length by a shallow furrow having its surface continuous with the surface of the stipe; cavity of the stipe nearly closed at the base of the arms by a thin diaphragm opening above into a closed chamber with dome-shaped wall even on its inner surface and adherent to the arms for about $\frac{1}{6}$ their length; gleba brownish olive-green, supported upon the dome and closely embraced by the arms; spores simple, olive-green, ellipsoidal, $\frac{1}{4} \times 1\frac{1}{2} \mu$, 5-8 on septate and constricted basidia.

Total height of plant 10-12 cm.; arms about \(\frac{1}{6} \) of this; greatest diameter of stipe 15 mm.

Hab. Near East Galway, New York (Burt), on a cultivated sandy hillside.

Although in its general aspect this fungus bears a certain external resemblance to Anthurus australiensis (Cooke and Massee) Ed. Fischer, as the latter is illustrated by Fischer in "Neue untersuch. phalloideen," Fig. 57, yet it differs from that species in the erect position; in structure of its arms; in having a dome-shaped chamber separated from the cavity of the stipe by a diaphragm; and in its slightly narrower spores.

From the Brazilian species, A. sanctae-catharinae Ed. Fischer, it differs in about the same characters and also in its white stipe.

It seems to approach more closely to another South American form, A. clarazianus (Müller) Ed. Fischer. It differs from this in being about four or five times as large; in not having the wall of the arms sharply differentiated in structure from that of the stipe; in having its stipe with a circular outline in cross section, while the form described by Spegazzini is noted by Fischer to have been indistinctly hexagonal; and in its smaller spores. Seven arms are sometimes also present in that species.

But it seems to be very distinct from the other species of Anthurus in its approach toward Lysurus. It is the only species of Anthurus at present known in the northern continents.

In conclusion, I desire to express my heartiest thanks to Prof. W. G. Farlow for the use of books from his library and for his direction in this research; and to Prof. R. Thaxter for his critical examination of certain preparations.

EXPLANATION OF THE PLATES.

Figures 4-23 were drawn with the aid of an Abbé camera lucida.

LETTERS COMMON TO ALL THE FIGURES.

- M, medullary tissue of axis of plant in young stages-occupies the space of the main central cavity of mature plant.
- M', gelatinous layer of peridium-of medullary origin.
- i, inner wall of peridium.
- C, cortical layer, or outer wall of peridium.
- C', cortical plates—portions of cortical layer not pushed outward by the extrusion of the medullary masses in the formation of M'.
 - ¹ Fischer: Neue untersuch. phalloideen, p. 28, taf.
- ² Fischer: Untersuch. phalloideen, p. 65.

6, fig. 40.

³ J. Müller in Flora, 1873, p. 526, and tab. 6, B.

- C", sheath of cortical tissue surrounding the fundament of the stipe.
- a, fundament of wall of the stipe, consisting of
 - b, hyphae of medullary origin in spaces which become cavities later and
 - p, hyphae of cortical origin which differentiate into pseudoparenchyma.
- a', fundament of the arm.
 - b', gelatinous tissue of arm of same nature and a part of b.
 - p', pseudoparenchymatous layer of arms of same nature as p.
- g, gleba.
- t, trama.
- h, hymenial layer.
- n, connection of gelatinous masses of peridium with M and not yet cut off by completion of inner wall of peridium, i.
- d, dome.
- j, diaphragm.

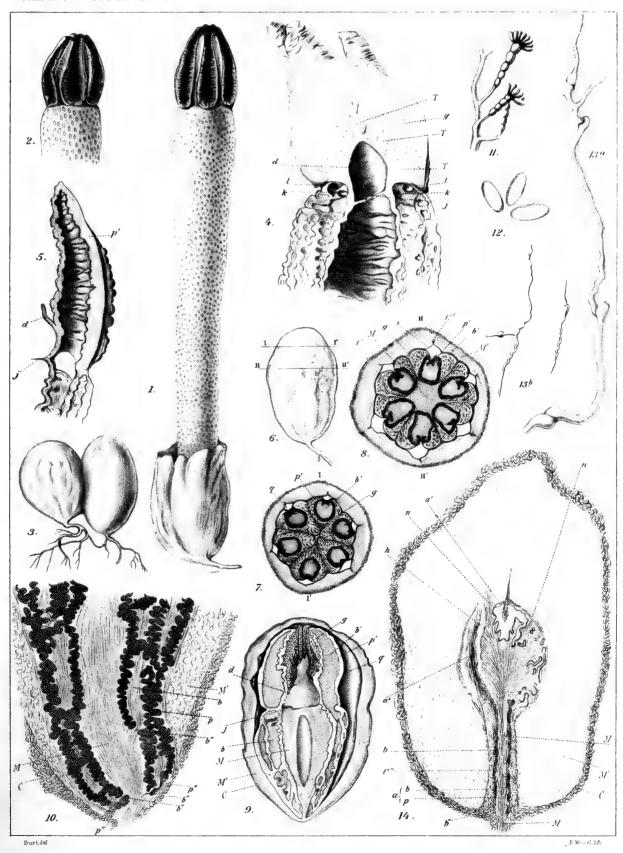
PLATE 49.

- Fig. 1. A plant which has passed its maturity. The removal or flowing away of the gleba discloses the cross wrinkles of the arms. Natural size.
- Fig. 2. Upper portion of a plant just at maturity. Gleba is in situ yet. Natural size.
- Fig. 3. Two eggs. Natural size.
- Fig. 4. Half of upper portion of a plant split longitudinally—the plane of division passing between the arms. Shows cavernous structure of the stipe. k, passage connecting adjacent cavities which are at the base of and alternate with the arms. l, passage leading into cavity of the arm. T, sheet-like masses of tramal tissue.
- Fig. 5. Half of an arm split longitudinally. Same lettering as before. x 21/2.
- Fig. 6. An egg in an advanced stage of development. Cross sections of this at two planes show the position of the gleba with respect to the arms. Slightly enlarged.
- Fig. 7. Cross section of above egg at plane I-I'. Gelatinous tissues are shaded alike. At q the separation of the volva from the arms and gleba has already occurred. The cortical plates C' have lost their connection with the arms and also with the cortical layer C. x about 2.
- Fig. 8. Another cross section at plane II-II'. x about 2.
- Fig. 9. Half of an egg in a very advanced stage of development split longitudinally. Separation of the volva from the receptaculum has taken place at q. The cavity of the stipe is also in formation. x 2\frac{1}{4}.
- Fig. 10. Median longitudinal section of an old egg, showing the folded structure of the pseudoparenchyma, p. At b'' hyphae of chamber are connected with the medullary tissue M of axis; pseudoparenchyma passes over into cortical layer C at p''. x 10.
- Fig. 11. Portion of a tramal hypha with 3 lateral branches terminating in basidia. The spores are omitted from one basidium. x 860.
- Fig. 12. Three spores. x 2400.
- Fig. 13. 13a, hypha from cortical layer showing enlargements or a form of clamp connections at the septa. x 325. 13b, hyphae from gelatinous layer of peridium, showing similar condition. x 325.
- Fig. 14. Longitudinal section of the youngest egg found. Lower part of figure was added from second section as the sections were cut very slightly oblique. At n the gelatinous masses M' are connected with the medullary tissue M. x 17.

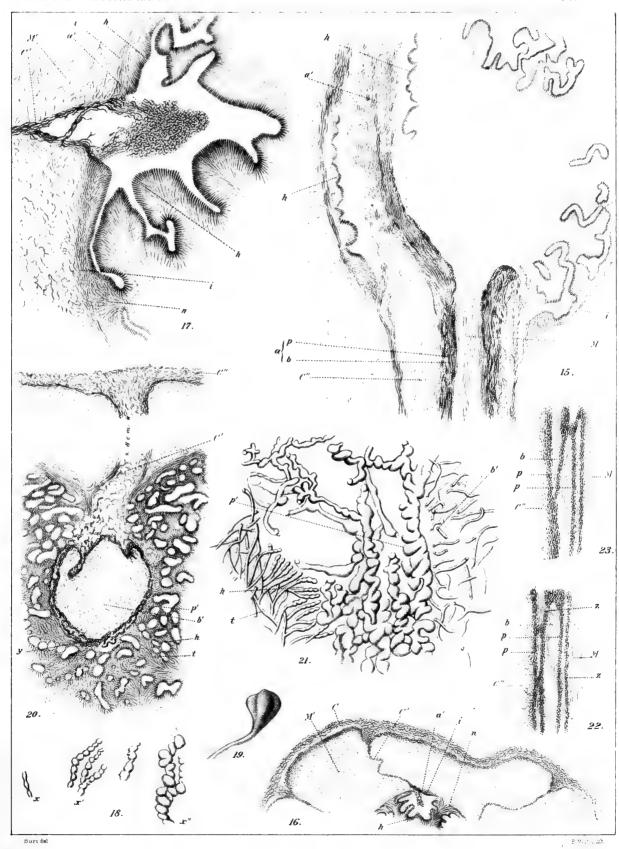
PLATE 50.

- Fig. 15. Portion of Fig. 14 more highly magnified and from a single section. x 60.
- Fig. 16. Cross section of half of the same egg, showing fundament of arm a', cortical plate C', etc. x 17.
- Fig. 17. Portion of Fig. 16 showing the series of folds and furrows in the gleba that are developing at the surface of the cavity in which lies the fundament of the arm a'. The hymenium is here a palisade-like layer of swollen hyphal ends h. The inner wall of the peridium is just beginning its development. x 60.
- Fig. 18. Pseudoparenchyma of the stipe in different stages of development. x and x' are from the egg figured in Figs. 14-17; x'', from that of Figs. 20-23. x 400.
- Fig. 19. Very young egg of Clathrus columnatus, having greatest diameter of 12 mm. Shows broad longitudinal ridges caused by extrusions of the medullary tissue M. x about 62.
- Fig. 20. Portion of cross section of egg in an intermediate stage of development. A portion of the cortical plate and gelatinous layer that would lengthen the figure 8 cm. has been omitted. x 34.
- Fig. 21. Part of wall of the arm from Fig. 20, y. Barren basidia are at h. x 670.
- Fig. 22. Radial longitudinal section of wall of stipe of same egg showing straight-walled chambers and connections z of medullary hyphae of one chamber with the other. x 60.
- Fig. 23. The following section of the wall. This alone might give the impression that the chambers have no connection with each other. x 60.









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ERRATA.

Page 18, line 5 and note 2, for Archimantis read Lithomantis.

Page 19, line 15, for Ledrophora read Legnophora.

Page 68, line 20, for internomedian read externomedian.

Page 138, heading, for Sytlactis read Stylactis.

Page 150, line 19, for arrayed read arranged.

Page 171, line 2, for figs. 16, 18 read figs. 16-18.

Page 240, 2d line of note, for Lisyra read Sisyra.

Page 299, 9th line from bottom, 1st column, for bretonensis read bretonense.

Page 323, line 29, for cold read coal.

Page 323, last line but one, for Palephemera read Platephemera.

Page 337, line 5, for στέφω read στρέφω.

Page 347, in centre, for Megantheutomum read Megathentomum.

Page 357, line 31, for non-existing read now existing.

Page 415, 5th line from bottom, for Agalma read

Page 416, lines 3, 11, 14, 18, for Agalma read Aglaura. Page 441, 8th line from bottom, for size read length.

Note by S. H. Scudder.—By an unfortunate accident, three of the species described in the memoir on Palaeozoic cockroaches have been ascribed to the wrong discoverer and to an incorrect horizon and locality. Necymylacris heros (p. 54, pl. 5, fig. 9), Archimylacris parallelum (p. 85, pl. 6, fig. 6), and the species described without a name (p. 128, pl. 6, fig. 13), were all discovered by Mr. R. D. Lacoe, and not by Mr. Mansfield, in the neighborhood of Pittston, Penn. Necymylacris heros, like the single other species of the same genus, was found in a heavy black shale in the lowest productive coal measures, or the roof shales of vein C. Archimylacris parallelum and the other species came from Campbell's ledge, near the bottom of the interconglomerate (Rogers, No. XII). It is due to these gentlemen to state that the mistake is entirely mine.



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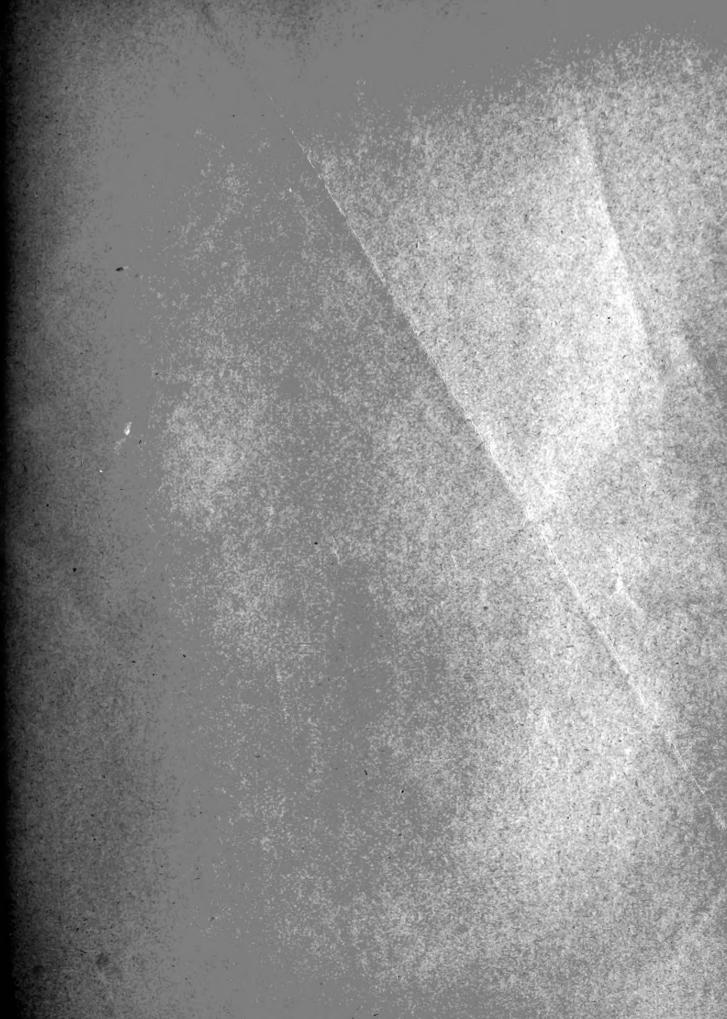
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